

TAXONOMIC STATUS OF *CORDYLANTHUS*
(SUBG. *DICRANOSTEGIA*) *ORCUTTIANUS*
(SCROPHULARIACEAE)

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Asa Gray (1883) described *Cordylanthus orcuttianus*, native to northern Baja California and adjacent California, in a monotypic section, *Dicranostegia*. Pennell (1947) raised the taxon to generic rank. Subsequently, the taxon has received scant attention except for treatment (as a genus) by Wiggins (1964) in his flora of the Sonoran Desert. We examined various aspects of the morphology and cytology of this species in conjunction with similar studies of all species of *Cordylanthus*. These comparative studies of flower and inflorescence, of pollen wall and seed coat patterns as observed with scanning electron microscope, and of chromosome numbers give evidence that this species should be retained in *Cordylanthus*, where it forms one of three subgenera. A taxonomic treatment of one of these three groups, i.e., subg. *Hemistegia*, is complete (Chuang and Heckard, 1973) and an infrageneric classification of subg. *Cordylanthus* that proposes division into sections is in preparation.

Cordylanthus is a member of the subtribe Castilleinae (tribe Rhinanteae) and stands apart from the other five members (*Castilleia*, *Orthocarpus*, *Clevelandia*, *Ophiocephalus*, *Gentrya*) of that subtribe (Breedlove and Heckard, 1970) on the basis of its spathe-like, usually bifid calyx.

All members of the subtribe are root-parasites; *C. orcuttianus* is a facultative root-parasite that has been successfully cultivated both with and without a host (Chuang and Heckard, 1971). Data on probable natural hosts of *C. orcuttianus* are meager but the plants are characteristically found in openings among shrubs and herbaceous perennials that are probable hosts. Whether there is a high degree of host-specificity that limits *Cordylanthus* to the geographic range of one or few hosts is unknown.

COMPARATIVE MORPHOLOGY

Cordylanthus orcuttianus has an indeterminate elongate spike (fig. 1 a), an unspecialized type of inflorescence characteristic of subg. *Hemistegia* and some species of subg. *Cordylanthus*.

The floral bract that subtends each flower of the spike is spathe-like with 1-3 pairs of linear-lanceolate lobes near the middle (fig. 1 c and d)

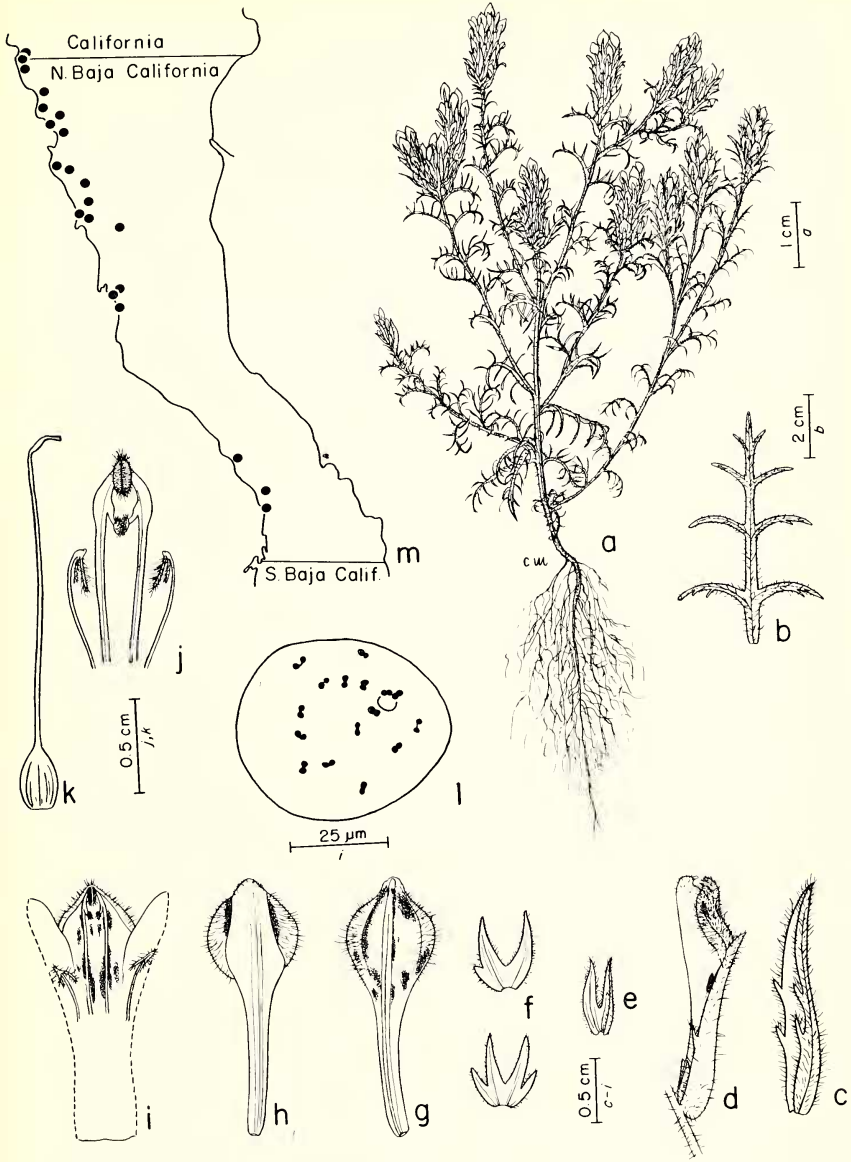


FIG. 1. *Cordylanthus orcuttianus*. a, habit; b, leaf; c, floral bract; d, flower e, calyx; f, variations of calyces; g, ventral view of flower with calyx removed; h, dorsal view of flower with calyx removed; i, flower opened dorsally; j, anthers; k, pistil; l, meiotic chromosome figure, $n=16$, diakinesis; m, distribution map. a-i and k-l from Moran 15392; j from Heckard 3240. Drawings by Charlotte Mentges.

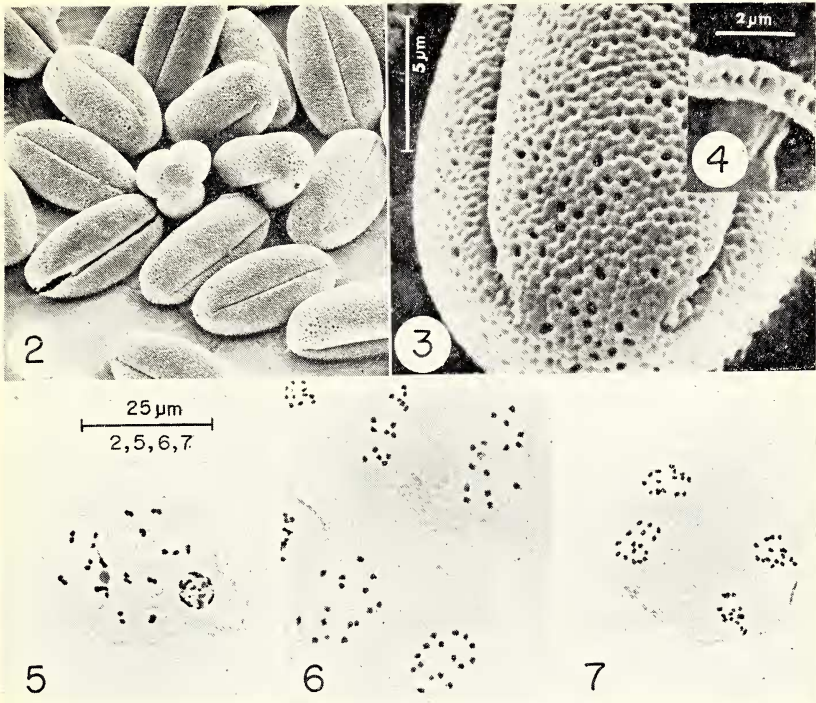
and resembles the bract found in some species of both subg. *Hemistegia* (Chuang and Heckard, 1973) and subg. *Cordylanthus*.

Cordylanthus has a distinctive spathe-like calyx usually about as long as the corolla and slightly bifid at the apex with a 1–2 mm slit or sometimes entire. In *C. orcuttianus*, however, the calyx is smaller ($\frac{1}{4}$ to $\frac{1}{3}$ the length of the corolla) and deeply bifid to $\frac{2}{3}$ its length, forming two attenuate lobes (fig. 1 d and e). The calyx surrounds the base of the corolla tube dorsally and laterally (fig. 1 d) but does not have a short basal tube as in some species of subg. *Cordylanthus*. Occasional flowers in an inflorescence of some plants raised from seed (Moran 15,392, JEPS) develop either 3- or 4-lobed calyces (fig. 1 f). These abnormal calyces have one or two extra, smaller or vestigial, anterior lobes, each of which is supplied with a vein.

The club-shaped corolla of *C. orcuttianus* (fig. 1 g and h) resembles that of other members of *Cordylanthus*. The stamens, however, are variously modified from those in the remainder of the genus. The dorsal pair are sterile, each with two heavily bearded vestigial anther sacs (fig. 1 i and j). Each stamen of the fertile ventral pair has an enlarged and elongated (2 mm) connective forming a slightly curved arm bearing a large anther sac attached medianly at the top of the connective and a smaller sac below at the end of a short spur (fig. 1 i and j), which is almost 1 mm long.

Cordylanthus orcuttianus, like *C. palmatus* (subg. *Hemistegia*), has seed with arching crests on the dorsal side. The seed is cochlidospermous, 1.0–1.5 mm long with strongly reticulate seed coat and irregularly scalari-form thickenings on the reticulum surface. Seed coat morphology of *C. orcuttianus* is in most respects similar to that of subg. *Hemistegia*, indicating a possible relationship between the two subgenera (Chuang and Heckard, 1972).

Pollen grains used for this study were obtained from herbarium specimens (Heckard 3240). For light microscopy, pollen samples were acetolyzed (Erdtman, 1960) and mounted in glycerine jelly. For scanning electron microscopy, dried pollen grains and sections were coated with gold under a conventional vacuum evaporator and then were examined and photographed with Cambridge Stereoscan Electron Microscope. For obtaining sections acetolyzed pollen grains were cut at 2–4 μm using a freezing microtome at -30°C . The general shape of *C. orcuttianus* pollen is prolate or subprolate in equatorial view, $24\text{--}27 \times 17\text{--}20 \mu\text{m}$, and rounded-triangular in the polar view. Grains are 3-colpate; colpi are long, with tapering ends (fig. 2). The exine is ca 1 μm thick and its surface is microreticulate and not uniformly perforate (fig. 3). The sexine is made up of bacula supporting the perforate tectum (fig. 4). From our preliminary investigation using SEM, pollen morphology appears to be fairly uniform throughout the genus, with 3-colpate and microreticulate exine.



FIGS. 2-7. Scanning electron micrographs of pollen grains and photomicrographs of chromosomes of *Cordylanthus orcuttianus*. 2. Equatorial and polar views of pollen grains. 3. Oblique view of grain showing unequally perforate tectum. 4. Sporoderm section of pollen grain showing foot layer, bacula, and tectum. FIGS. 5-7. Meiotic chromosome figures, $n = 16$. 5. Diakinesis. 6. Prophase II. 7. Telophase II.

CYTOLOGY

Cordylanthus orcuttianus has $n = 16$ (figs. 1 1, 5, 6, and 7). Meiosis was regular in several aceto-carmines squashes of pollen mother cells fixed in acetic acid-ethanol (1:3, v/v). A sampling was made from several plants raised in the greenhouse from a single general seed collection (Moran 15,392). Other chromosome counts for the genus are $n = 14, 15$, and 21 for subg. *Hemistegia* (Chuang and Heckard, 1973) and $n = 12, 13, 14$ (unpublished data) for subg. *Cordylanthus*. The diversity of chromosome numbers within the genus is a useful adjunct to other information in *Cordylanthus* taxonomy and each number (except $n = 14$) coincides with one particular group of related species.

DISCUSSION AND CONCLUSIONS

Our comparative studies do not support Pennell's view (1947) that *C. orcuttianus* deserves generic status. Basic features setting *Cordylanthus*

apart from its closest relatives in Castilleiinae—namely, the club-shaped corolla and the 2-lobed, one-sided calyx—occur also in *C. orcuttianus*. Seed-coat and pollen-wall features are also similar. The only features consistently different from those in other members of *Cordylanthus* are the deeply pinnately dissected leaves, the smaller and more deeply cleft calyx, the elongated connective that separates pollen sacs of the anther, and the chromosome number, $n = 16$. The only morphological difference mentioned by Pennell was that of the calyx. He also pointed out that the plants flowered in spring while the other species were summer and early fall bloomers. While it is true that *C. orcuttianus* flowers earlier, its flowering period extends also into late summer. *Cordylanthus maritimus* Nutt. ssp. *maritimus* (subg. *Hemistegia*) begins flowering in May, only a month later than for *C. orcuttianus* growing in the vicinity, the Mexican border at Tijuana.

Most morphological differences of *C. orcuttianus* are only variations in degree of features found in other members of the genus. In some instances features of *C. orcuttianus* are most likely primitive in the genus, as in the case of the pinnately dissected leaf and deeply cleft calyx, but the elongated anther-connective and chromosome number of $n = 16$ seem to be derived conditions. Although pinnately dissected leaves are limited to this species in the genus, bracts and upper cauline leaves are shallowly pinnately lobed in *C. mollis* (subg. *Hemistegia*), as are bracts in *C. kingii* (subg. *Cordylanthus*). We interpret the pinnately dissected leaf as primitive in Castilleiinae, since it is found in presumably primitive species of *Castilleia* (Holmgren, 1971) and *Orthocarpus*. We agree with Pennell (1947) that the calyx of *C. orcuttianus* is less modified than that of other species in the genus, which have extensive fusion of the two lateral lobes. The apex of the calyx is deeply divided only in *C. orcuttianus* and, about half as far, in *C. capitatus* (subg. *Cordylanthus*).

The calyx of *C. orcuttianus* is completely divided to the base ventrally and $\frac{2}{3}$ of its length dorsally (fig. 1 e). We postulate that it evolved by modification of the typical 4-lobed calyx of Castilleiinae. Such a 2-lobed calyx could arise by division of the tube ventrally and fusion of each pair of lobes to form only two lobes. The abnormal 4-lobed calyx (fig. 1 f) seen in greenhouse plants and described earlier may evidence a 4-lobed stage in evolution of the *Cordylanthus* calyx. Pennell (1947) postulated development of the calyx in much the same way and believed that further evolution uniting the lobes dorsally and elongating them wholly on the upper side formed the calyx found in the rest of the genus. He suggested that the resultant calyx was so different that the two types could not satisfactorily be included within the same genus. We see them, however, as basically the same type of calyx, representing different stages in evolution of the completely united spathe-like calyx.

The elongated connective of the anther (fig. 1 j) was not mentioned by Pennell (1947) but is a novel feature of the species and undoubtedly

is a modification of the condition in Castilleiinae in which the small connective bears two unequal anther sacs, a large one attached medianly and a smaller one attached apically. In the functional stamens of *C. orcuttianus*, the anthers are unequal in size but the connective is considerably enlarged, resulting in a strikingly modified stamen. Reduction of the dorsal stamens has occurred independently in all three subgenera.

Although the chromosome number, $n = 16$, of *C. orcuttianus* is unique in the genus, differences in chromosome number are not necessarily evidence of generic separation. All numbers from $n = 12$ to 16 (plus 21) are found in *Cordylanthus*.

TAXONOMY

Cordylanthus Nutt. ex Benth. subg. ***Dicranostegia*** (A. Gray) Chuang & Heckard, stat. nov.—*Cordylanthus* sect. *Dicranostegia* A. Gray, Proc. Amer. Acad. Arts 19:95. 1883.—*Adenostegia* sect. *Dicranostegia* (A. Gray) Ferris, Bull. Torrey Bot. Club 45:417. 1918.—*Dicranostegia* (A. Gray) Pennell, Proc. Acad. Nat. Sci. Philadelphia 99:189. 1947.—TYPE SPECIES: *Cordylanthus orcuttianus* Gray.

Plants of coastal and desert scrub communities. Leaves deeply pinnately dissected with linear lobes. Inflorescence a dense spike. Floral bracts oblong-lanceolate with 1–3 pairs of pinnately arranged linear lobes. Calyx short, less than $\frac{1}{2}$ as long as corolla, deeply divided into two attenuate lobes, surrounding only the lower corolla tube dorsally and laterally. Stamens 4, the ventral pair fertile with elongated connective bearing 1 anther sac at either extremity; the dorsal pair sterile with aborted anther sacs. Seed deeply reticulate.

CORDYLANTHUS ORCUTTIANUS A. Gray, Proc. Amer. Acad. Arts 19:95. 1883.—*Adenostegia orcuttiana* (A. Gray) Greene, Pittonia 2:181. 1891.—*Dicranostegia orcuttiana* (A. Gray) Pennell, Proc. Acad. Nat. Sci. Philadelphia 99:190. 1947.—TYPE: Mexico: Baja Calif., “about 70 miles below the U.S. boundary, H. C. Orcutt and son”. (Holotype: GH!; isotype: K!) Identity of the type specimen of *C. orcuttianus* is questionable, perhaps due to a labeling error. Although Gray (1883) described the type locality as “70 miles south of the border”, the only collection seen by us that was made by H. C. Orcutt and son prior to the 1883 publication date is one labeled as “Tia Juana Lower Calif., 1883, H. C. Orcutt & Son” (GH!). The two unusually small plants agree with Gray’s description of the plants as “only 6 inches high, mostly branched from the base”. A single, similar plant with the label (probably in Gray’s hand) “Lower California, Orcutt, 1883—Ex Herb. A. Gray 1/1884” is at K(!). No specimen from “70 miles south of the border” was found, indicating to us that the 1883 collection is the type and that it was labeled rather casually (or erroneously) as from “Tia Juana”.

Annuals 20–35 (10–50) cm tall, divaricately branched mostly from near the base with several to many ascending or decumbent branches; herbage green or often suffused with dark red, densely to sparsely hirsute. Leaves 3–6 (2–8) cm long and 3–5 cm broad, pinnately dissected with 4–5 pairs of linear to subulate segments 1.0–1.5 mm broad, rachis up to 3.5 mm broad, occasional lower segments slightly lobed. Inflorescences of dense spikes 2–10 cm long, 2–3 cm broad, subtended by outer bracts. Floral bracts 1.5–2.5 cm long, oblong-lanceolate with 1–3 pairs of linear ascending lobes 0.5–1.5 cm long, 3-veined, hirsute along margins and veins. Calyx ca 6 mm long, divided to over $\frac{1}{2}$ its length into 2 attenuate lobes ca 4 mm long, occasionally forming 4 or 3 lobes with lateral ones smaller, each lobe 3-veined, hirsute along margins and veins, the base of calyx partially surrounding the base of corolla tube dorsally and laterally. Corolla club-shaped, two-lipped, 1.8–2.5 cm long, exceeding the floral bracts, the tube slightly exceeding the throat, white with lips yellow-tipped, the throat conspicuously inflated laterally, ca 6 mm broad; upper lip galeate and rounded apically with lateral margins enclosing the style and coherent anthers; lower lips 4 mm long, with dark red margins and scattered flecks of dark red extending back along the white throat; galea puberulous dorsally, the lower lip and throat velutinous. Stamens 4, didynamous, ventral pair fertile with elongated connective forming a bent arm bearing one anther sac at either extremity, the upper anther sac larger, ca 1.2 mm long, hirsute at both ends; lower sac smaller, ca 0.5 mm long, densely hirsute; upper pair of stamens sterile, the vestigial anther sacs represented by two hyaline, villous appendages; filaments glabrous; style elongate, the tip bending downward and emerging through apical notch in galea, the stigma barely exposed. Seeds dark brown, 1.0–1.5 mm long, irregularly reniform, deeply reticulate with conspicuous arching crest on dorsal side, 32–40 in each capsule. Chromosome number $n = 16$.

HABITAT AND DISTRIBUTION (fig. 1 m): Along sandy arroyos, washes, and on slopes and plains in openings among shrubs, as *Ambrosia*, *Atriplex*, *Virguieria*, *Bebbia*, and *Solanum*; largely coastal, just north of United States border in San Diego County, California, and in N Baja California of Mexico south to the vicinity of Miller's Landing, just north of latitude 28°N; sea level to ca 350 m; flowering April to July (March to September).

REPRESENTATIVE SPECIMENS: UNITED STATES: California: San Diego Co.: 2 mi E of San Ysidro on Otay Mesa, *Gander 219.21* (SD).

MEXICO: Baja California: boundary line near Monument 258P, *Mearns 3927* (DS); S of Tijuana, *Pennell & Epling 25200* (CAS, F, NY, PH, UC); 6 mi NE of Descanso, *Wiggins & Thomas 351* (DS); 3 mi E of La Mission, *Moran 13156* (RSA, SD, UC); 2.5 mi NW of San Antonio, *Moran 13948* (DS, SD); Sauzal, *Orcutt & Fish s.n.* (MO, US); Ensenada, *Brandegge s.n.* (UC); Arroyo Santo Tomas, *Wiggins & Thomas 402* (DS); near San Jacinto, *Gander 7308* (SD); S of San Vicente,

Pennell & Epling 25254 (NY, PH, UC); San Antonio del Mar, *Gander 7358* (SD); Colnett, *Moran 13999* (SD); 6.5 mi W of Rancho San José, *Wiggins 10046* (DS, UC); 10 mi E of Santa Margia, *Moran 11011* (SD); 10 mi S of San Quintín, *Harbison 41819* (PH, RSA, SD); El Socorro, *Moran 15392* (ISU, JEPS, SD); 7 mi SW of Punta Prieta, *Heckard et al. 3240* (JEPS, ISU); 5 mi N of Miller's Landing, *Wiggins 5727* (CAS, DS, F, NY, POM, RM, UC).

ACKNOWLEDGMENTS

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SALSOLA SODA L. (CHENOPODIACEAE) IN CENTRAL CALIFORNIA.—This species, sometimes known as Glasswort, is a native of southern Europe, and has become established in several localities around the margins of San Francisco Bay. In some places, as the Palo Alto Yacht Harbor, it is very common. It can be expected to spread in California. The standard floras for California (P. A. Munz', *A California flora*, 1959; *Supplement*, 1968; and *A flora of Southern California*, 1974, all University of California Press, Berkeley) do not record this species nor do two recent papers (J. T. Howell, *Miscellaneous notes on Munz' A California flora and Supplement*, *Wasmann J. Biol.* 30:97-107, 1972; J. C. Beatley, *Russian-thistle (Salsola) species in western United States*, *J. Range Managem.* 26:225-226, 1973). It would appear that *Salsola soda* is a new introduction into western North America and perhaps for the entire continent. Specimens seen so far from California are: Alameda Co.: Alameda, *Long s.n.*, 6 Oct 1971 (CAS); *Long s.n.*, Nov 1971 (CAS). San Mateo Co.: W end Dumbarton Bridge, *Anderson s.n.*, 25 Jul 1968 (CAS); *Anderson s.n.*, 16 Aug 1968 (CAS); *Thomas 14860*, 7 Dec 1968 (DS); Palo Alto Yacht Harbor, *Thomas 17615*, 6 Oct 1974 (DAO, DS, MO, OCS, RSA). Santa Clara Co.: Palo Alto Yacht Harbor, *Thomas 17603*, 22 Sep 1974 (DS, JEPS).—JOHN H. THOMAS, Department of Biological Sciences, Stanford University, Stanford, California 94305.